THE DISTRIBUTION PATTERNS OF NORTHERN AND SOUTHERN ELEMENTS IN THE FLORA OF NEWFOUNDLAND[1]

by

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Introduction

The flora of the Island of Newfoundland has attracted much attention, mainly as a result of the explorations of Fernald (1911, 1918a, 1918b, 1924, 1925) in the beginning of this century. The vivid descriptions of his field trips, and especially his explanation of the origin of the Newfoundland flora, have focused the attention of plant geographers on the island and the general region of the Gulf of St. Lawrence. His theories have had a great impact on plant geographical thinking in America as well as Northern Europe.

The most conspicuous features of the flora of Newfoundland Rouleau, 1956; Arsène, 1927) are the occurrence of many species with arctic affinities, the absence of many temperate-boreal species present on Cape Breton Island, and the common occurrence of the so-called Coastal Plain species, very often in close association with the arctic species. In addition, the flora contains a number of species which have their main distribution area in western North America. This Cordilleran element is mainly restricted to the mountains and unstable soils of western Newfoundland.

Most of the data on species distribution in Newfoundland, used in this paper, were obtained by personal observation and collection. However, I am grateful to Dr. E. Rouleau of the University of Montreal for showing me many of his unpublished distribution maps of Newfoundland vascular plants. These maps were particularly helpful in checking

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[1]Department of Forestry, Canada, Forest Research Branch Contribution No . . .

my observations on the absence of a species from certain parts of the island. Some published accounts of botanical expeditions, in particular those of Fernald (1926, 1933), provided useful additional information on the distribution of a few rare speces.

Thanks are also due to Dr. T. Ahti, University of Helsinki, Dr. W. S. Benninghoff, University of Michigan, Dr. T. C. Brayshaw and Dr. J. S. Rowe, Department of Forestry of Canada, and Dr. W. S. Maass, National Research Council, for helpful suggestions and valuable criticism on a draft of the manuscript, and to Dr. M. E. Hale, Smithsonian Institution for identification of some of the lichens.

In this paper an attempt will be made to analyse the southern and northern elements in the flora of Newfoundland. Before doing this, it will be necessary to describe briefly the geography of the island.

Geographic Setting

The Island of Newfoundland is located off the east coast of the American continent between 46°30′ and 51°30′ N. Lat. and between 59°30′ and 52°45′ W. Long. It covers an area of a little over 42,000 square miles. It is separated in the southwest from Cape Breton Island by the Cabot Strait, and in the northwest from Labrador by the Strait of Belle Isle, 70 and 11 miles wide at their narrowest points respectively (Figure 1).

The island consists essentially of a tilted plateau of moderate to slight relief. It rises gradually to the west, where elevations of over 2,500 feet can be found.

Calcareous soils and limestone outcrops and cliffs prevail along the west coast from St. George's Bay to the northernmost tip of the Great Northern Peninsula. Acidic bedrock, and glacial till derived from it, cover most of the remainder of the island. Serpentine mountains occur along the west coast, between St. George's Bay and Bonne Bay, and also in the northern part of the Great Northern Peninsula.

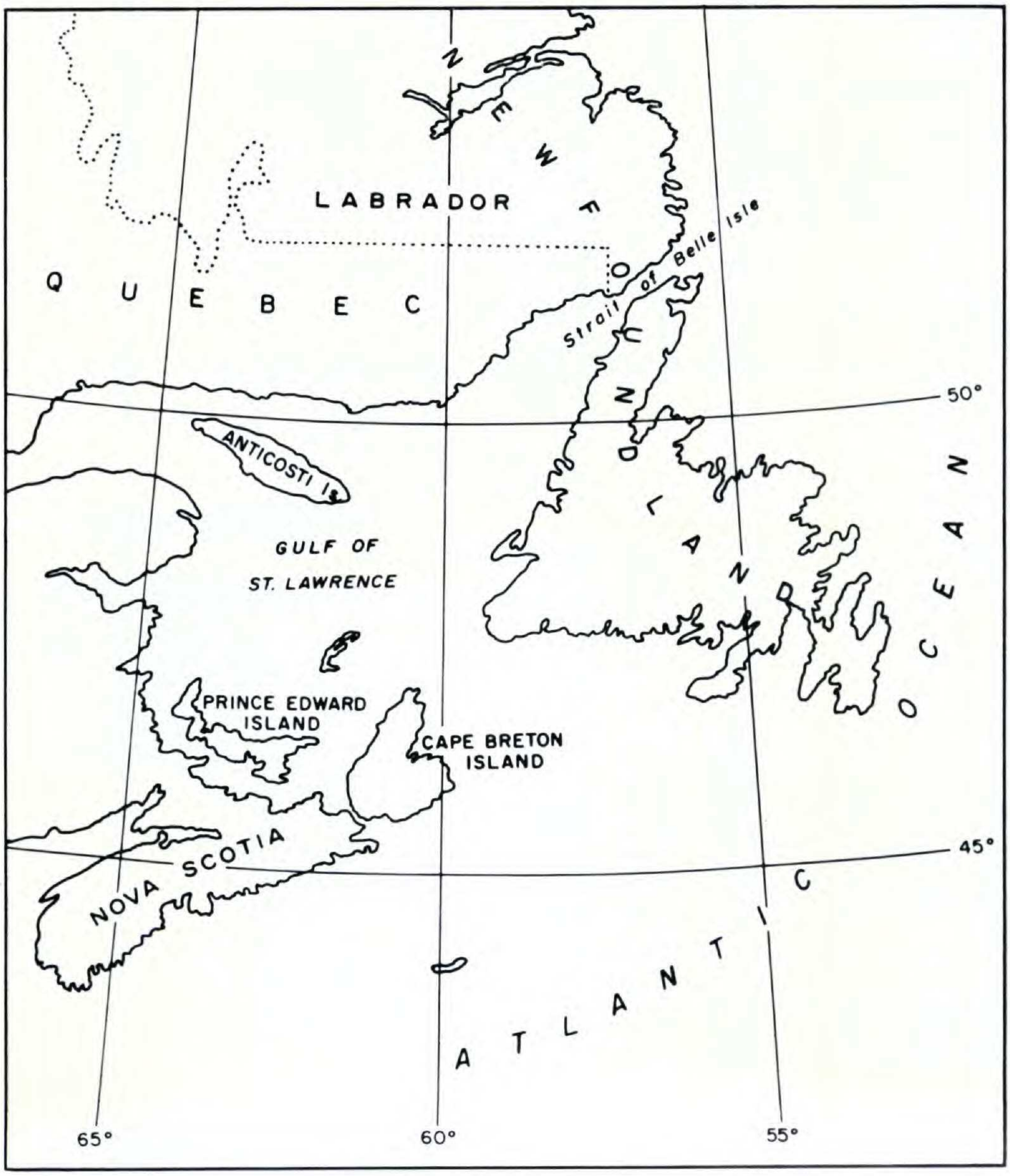

Figure 1. Location of the Island of Newfoundland in relation to the American continent.

In spite of its location, the island does not have a hyper-oceanic climate. Southwestern and western winds prevail throughout the year. Consequently, the climate is greatly influenced by the American continent. This is clearly emphasized by the occurrence near the coast of many species considered continental or sub-continental in Europe, e.g., *Chamaedaphne calyculata*, *Rhododendron lapponicum*, and

many others. Therefore, the climate of the coastal areas should be considered sub-oceanic at most.

The cold Labrador Current flows along the shores of Newfoundland; this current brings ice floes along the shores in winter and spring, and icebergs during spring and summer. The coastal ice fields greatly retard the arrival of spring (Figure 2). The vegetative period starts from 30 to 50 days later in Newfoundland than in Montreal (Hare, 1952).

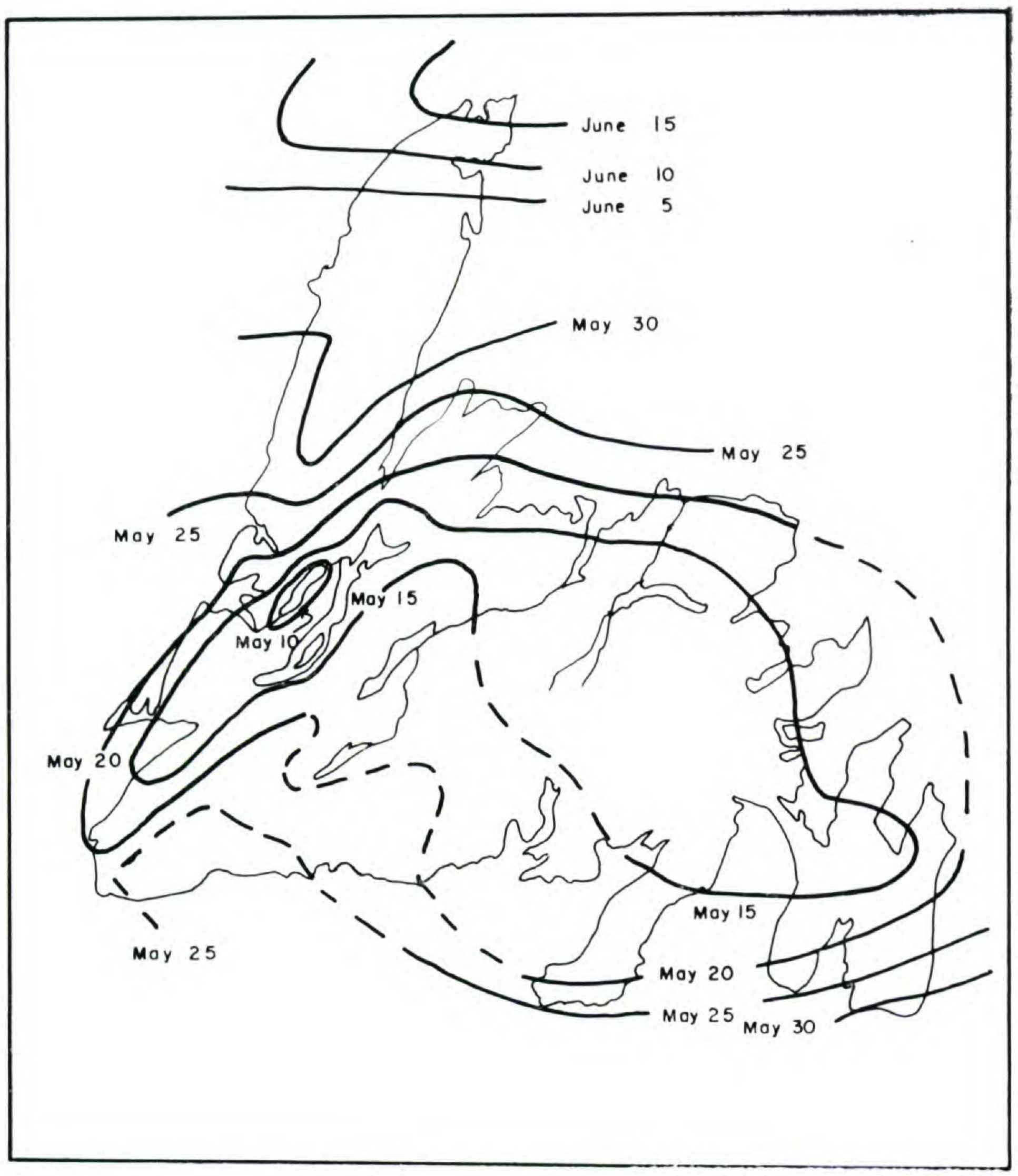

Figure 2. Start of vegetative season based on threshold temperature of 43°F. (After Hare 1952)

Very low summer temperatures prevail along the coast owing to the frequent occurrence of fog and the cooling effect of the sea; this phenomenon is particularly pronounced in the southern and southeastern parts of the island (Figure 3).

In winter, the sea has a moderating effect on the temperatures; the winters of Newfoundland are considerably milder than those of the adjacent continent. This is es-

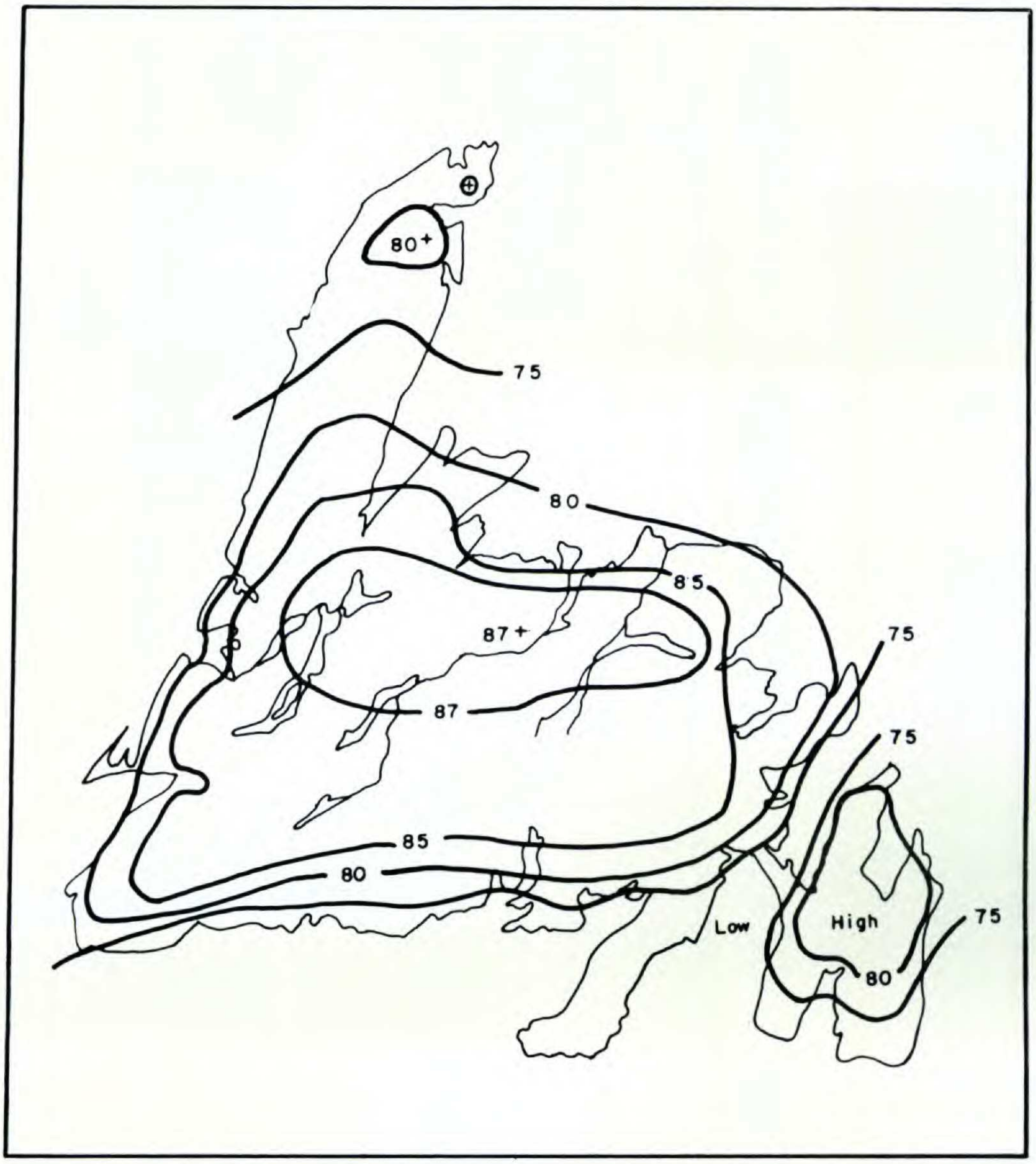

Figure 3. Mean annual maximum temperature in °F. The isotherms have been drawn on the basis of sea level temperatures, and thus show the temperature irrespective of elevation.

pecially true for the areas along the ice-free south coast and the Avalon Peninsula which is not usually surrounded by ice until March (Figures 4 and 5).

The precipitation is well distributed throughout the year in all parts of the island. It ranges from over 55 inches in the southern and southwestern parts to less than 35 inches in the northern areas. The driest area, with a precipitation of 30 inches, is found in the northwestern tip of the Great Northern Peninsula.

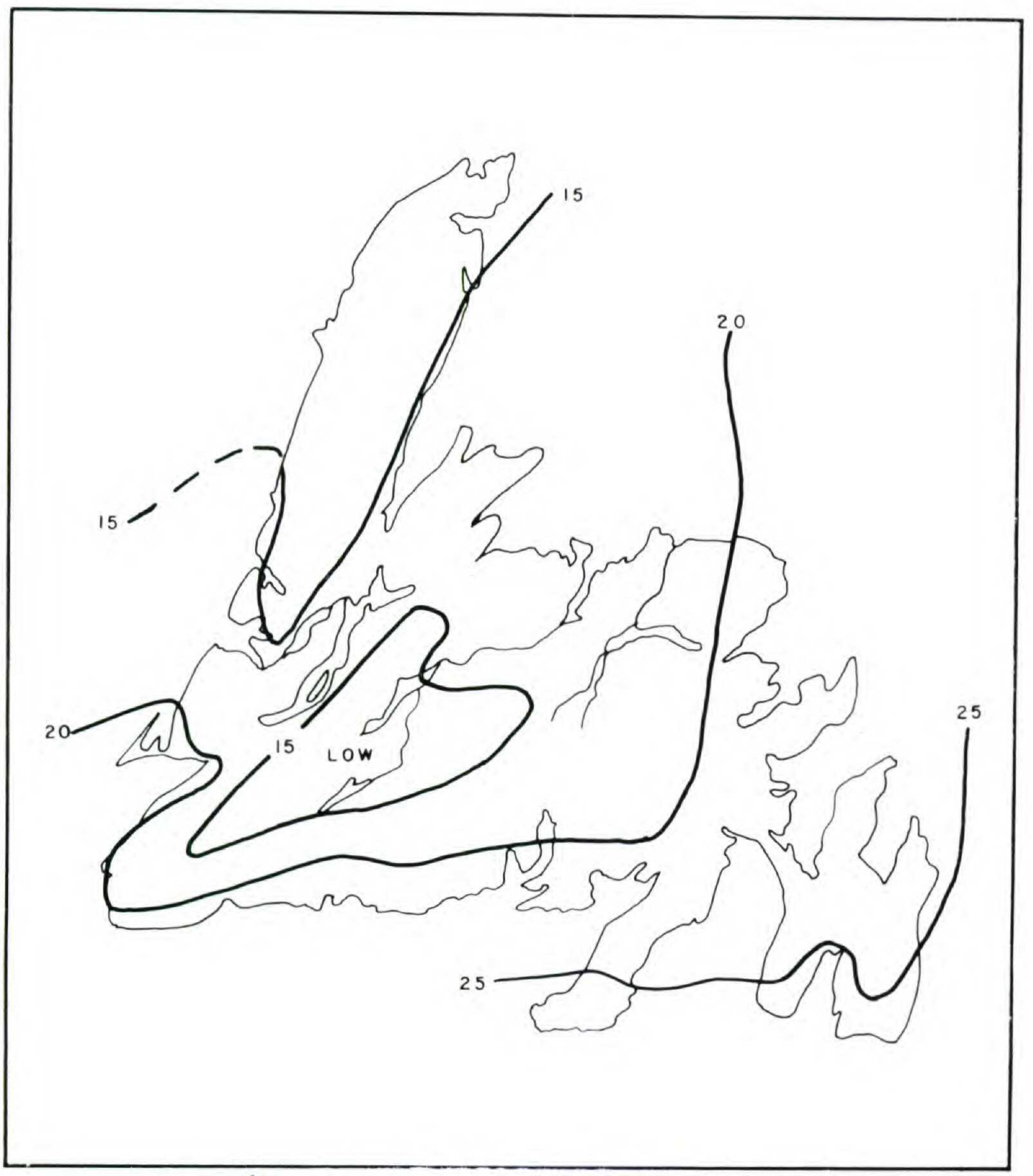

Figure 4. Mean monthly minimum temperature for January in °F. (After Hare 1952)

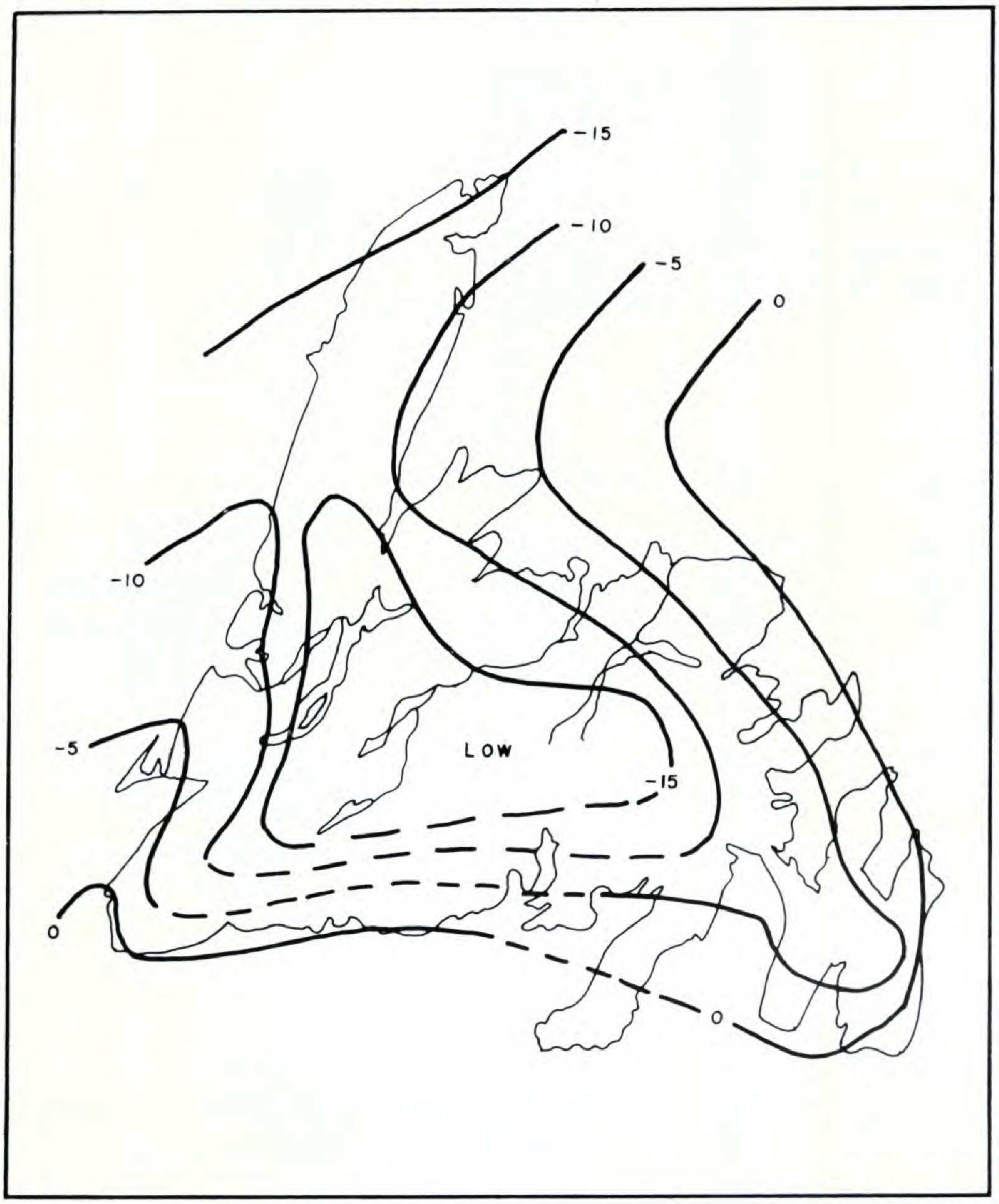

Figure 5. Mean monthly minimum temperature for January in °F. (After Hare 1952)

The island is situated within the Boreal forest region (Rowe, 1959). The central and western parts are heavily forested with treeless barrens restricted to the higher elevations. Most of the southern and eastern parts are covered by dwarf shrub heath and bogs (Ahti, 1959).

Plants with Southern Affinities

This group includes the so-called Coastal Plain element, a group of species restricted to oligotrophic bogs and dry sandy soils, and occurring southward along the Atlantic coast to the pine barrens of New Jersey. Although it is the most talked-about element, it is by no means the only southern element in the flora of Newfoundland; temperate-boreal species of both Canadian and Alleghanian range also occur.

The southern element is defined here to include those species occurring in Newfoundland but having their main range south and west of the island, and whose continuous range on the Canadian mainland does not reach as far north as southern Labrador. Thus defined, the southern element includes those species which, under the present climatic conditions, can reach Newfoundland only across the Cabot Strait; a point of interest in Fernald's theories on the origin of the Newfoundland flora, and in the discussion in the final part of this paper. A few species belonging to the southern element, as defined above, but occurring rather commonly up to the northern tip of the Great Northern Peninsula have been left out of consideration in the following discussion.

What are the ecological factors controlling the distribution of southern species in Newfoundland? Both climatic and edaphic factors are important in this respect; they will be briefly discussed below before describing the types of distribution to be found on the island.

CONTROLLING FACTORS

1. SUMMER TEMPERATURES AND LENGTH OF VEGETATIVE SEASON. Most of the southern plants have the main part of their range in areas with considerably warmer summers and a longer vegetative season than that found in Newfoundland. Therefore, this is the most obvious factor controlling their distribution. Species thus controlled will either show a clear northern boundary in Newfoundland, or they are restricted to some of the warmer valleys and sites.

It is worth mentioning that the areas with the longest and generally warmest vegetative season do not coincide with those with the highest annual maximum temperatures. The former occur in the valleys of the southern part of the west coast, whereas the latter are found in the northern central parts of the island. The annual maximum temperatures do not appear to be a relevant factor in determining the distribution of southern plants; at least, no species were found whose distribution was closely related to it.

2. WINTER TEMPERATURES. Most of the southern species reaching Newfoundland have a range extending far into areas with a much more continental climate. Therefore, they are adapted to winters much colder than those of Newfoundland, and it is obvious that low winter temperatures will not prevent any of these species from occurring on the island.

On the other hand, many species sensitive to low winter temperatures will be able to grow in Newfoundland because of the relatively mild winters of the coastal areas. These species concentrate especially on the southeastern peninsulas and along the south coast.

3. SPRING TEMPERATURES. One of the typical features of a continental climate is the rapid change from winter to summer, and the absence of a long period with alternating cold and warm spells so frequently encountered in northern oceanic climates. The occurrence of a cold spell following a mild period can be very detrimental to species which start their growing season as soon as the first mild days occur. This factor probably limits the distribution of a large number of continental species.

The phenomenon of a spring with alternating cold and mild spells is most common in the typically oceanic parts of the Island, e.g., the south coast and the eastern peninsulas, but it is also of great importance in central Newfoundland and along the northern shore. The west coast is the area most favorable for species sensitive to this factor.

4. SOIL CONDITIONS. Edaphic factors play an important role in determining the distribution of plants. The distribution of calcareous soils causes the greatest regional differences in the flora of Newfoundland, and many southern plants are restricted to western Newfoundland for this reason only.

Nutrient-rich soils are also more abundant in the western parts, but, although this limits the frequency of occurrence, it will rarely eliminate a species completely from the infertile eastern parts.

Dry, sandy soils also are warm soils, and a few southern species with low nutrient and moisture requirements can be found exclusively on these sites. A few other southern species occur only on unstable talus or terrace slopes and other sites with limited competition.

5. BIOTIC FACTORS. Some species are so dependent on the habitat condition created by the plant community in which they grow that the absence of one or more of their dominant associates can be the factor limiting their distribution. This factor is indirectly controlled by the climate. An extreme example of this kind of dependence is given by a number of liverworts, such as *Mylia anomala* and *Odontoschisma sphagni*, which occur almost exclusively in clumps of *Sphagnum fuscum* and *S. rubellum*. In analogy with this, it is quite possible that the occurrence of many species of northern hardwood forests, such as *Erythronium americanum*, *Medeola virginiana*, *Uvularia sessilifolia*, and *Sanguinaria canadensis*, are dependent on the occurrence of this type of forest. Sugar maple-yellow birch forests occur locally on rich soils in Cape Breton Island but they are lacking on Newfoundland, and with them many species characteristic of this forest type.

TYPES OF DISTRIBUTION

It will be obvious, that the distribution of the southern species is rarely limited by any single factor but as a rule

the result of the simultaneous action of several of them. The following distribution types can be recognized:

A. COMMON OR FREQUENT THROUGHOUT BUT ABSENT ON THE GREAT NORTHERN PENINSULA AND AT HIGHER ELEVATIONS.

This group is clearly limited by the length and warmth of the vegetative season. A large number of species belong to this group only a few of them are mentioned below.

Osmunda regalis
Trillium cernuum
Dulichium arundinaceum
Carex intumescens
Carex debilis
Carex gracillima
Carex crinita
Carex castanea
Corylus cornuta
Nemopanthus mucronatus[2]
Viburnum cassinoides[2]
Diervilla lonicera
Nymphaea odorata[2]
Aster umbellatus
Sambucus pubens
Alnus rugosa
Prunus virginiana
Vaccinium macrocarpa
Senecio aureus
Solidago rugosa
Acer rubrum
Pogonia ophioglossoides
Arethusa bulbosa
Rhododendron canadense[2]
Cypripedium acaule

B. RESTRICTED TO THE WEST COAST SOUTH OF DEER LAKE, THE DEEPER INLETS OF THE SOUTH COAST, NOTABLY BAY D'ESPOIR, AND SHELTERED PARTS OF THE SOUTHERN AVALON PENINSULA.

This group is also clearly limited by the length and warmth of the vegetative season, but its species demand somewhat higher summer temperatures than those of group A.

Betula lutea
Agrimonia striata
Scutellaria lateriflora

C. RARE OR LOCALLY OCCURRING SPECIES WHOSE DISTRIBUTION IS CLEARLY LIMITED BY LENGTH AND WARMTH OF THE VEGETATIVE SEASON.

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[2]Species extremely rare on the Great Northern Peninsula.

a. Restricted to Warm, Favorable Locations on the West Coast.
(Extreme examples of groups A and B.)
Claytonia caroliniana
Geranium robertianum
Fraxinus nigra (always as a small tree or shrub)
Cornus alternifolia

b. Limited to a Few Dry, Sandy Areas in Central Newfoundland. Most likely these are relic species for it is difficult to understand how they could otherwise have reached their present locations. This applies particularly to *Pinus resinosa*.
Carex houghtonii
Pinus resinosa
Gaultheria procumbens

c. Halophytes Restricted to Southwestern Newfoundland. The water of the Gulf of St. Lawrence is considerably warmer than that of the other coasts. It could well be that this rather than the air temperature determines the distribution of these species.
Scirpus validus
Spartina pectinata
Scirpus maritimus[3]

d. Very Scattered, but Clearly Limited by the Length of the Vegetative Season.

Typha latifolia — This species is restricted to a relatively warm belt extending from Port-aux-Basques along the west coast to Bonne Bay, and then to the northern part of Central Newfoundland; it occurs also in the central parts of the Avalon Peninsula.

D. RESTRICTED TO WESTERN NEWFOUNDLAND, SOUTH OF BONNE BAY.

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[3]New addition to the Newfoundland flora discovered by the author in a salt marsh near Boswarlos, Port au Port Bay, during the field season of 1961.

This type of distribution appears to be caused by two sets of conditions:

a. The Occurrence of Calcareous or Highly Basic Soils.

Cypripedium reginae *Dryopteris robertiana*
Scirpus acutus *Salix glaucophylloides*

b. Rather Continental Course of Spring Temperatures.

Epigaea repens is the most conspicuous example of this. The species occurs very commonly in western Newfoundland south of Bonne Bay, and even reaches rather high elevations at the east side of the Lewis Hills and in the mountains east of Grand Lake. It is very rare in the forested interior around Red Indian Lake and Victoria Lake. At high elevations the species is restricted to sites well covered with snow in winter and early spring. Consequently, it starts its vegetative period very late, and at a time that severe cold spells are unlikely to occur.

An example of a similar protection against early sprouting is seen in *Smilacina racemosa*[4]. It occurs in an *Alnus crispa* thicket on the southwest slope of the Lewis Hills at about 1000 feet elevation. It is not a particularly warm site, but it is usually covered with snow until the middle of June. Moreover, the conditions on the forest floor show an interesting resemblance to those of a hardwood forest.

E. CONCENTRATED IN SOUTHEASTERN NEWFOUNDLAND, THE SOUTH COAST, AND THE BOGS OF THE CARBONIFERIOUS SANDSTONE AREA OF ST. GEORGE'S BAY, BUT ALSO PRESENT IN BOGS ON THE WEST COAST MOUNTAINS AND OF THE INTERIOR BARRENS.

This group includes the Coastal Plain species. They are moderately oceanic species, apparently sensitive to low winter temperatures, adapted to cool summers, and possibly requiring a high air humidity. Only some of the bog and

[4]Recent addition to the Newfoundland flora; discovered by the author in 1961. In 1963, Dr. E. Rouleau (oral communication) found this species in an *Alnus rugosa* swamp along Mollichicnic Brook, Western Newfoundland.

pond species of this group occur, rather sparingly, at the higher elevations. In these areas, as in the coastal areas, snow drifting is severe in winter time, and thick snow layers cover the valleys and depressions. The occurrence of these species at higher altitudes could well be dependent on this protective snow cover.

The species with a very conspicuous concentration in the oceanic parts of the island, i.e., on the Avalon Peninsula, the Carboniferous sandstone area of St. George's Bay, and to a lesser degree along the south coast, are listed under b.

a. *Schizaea pusilla*
Myriophyllum tenellum
Nymphoides lacunosa
Utricularia geminiscapa
Sphagnum molle[5]
Sphagnum strictum[5]
Potamogeton oakesianus
Xyris montana
Bartonia paniculata
Aronia floribunda
Juncus militaris
Juncus pelocarpus
Scirpus subterminalis

In contrast to the other species of this group, both *Sphagnum molle* and *Sphagnum strictum* have never been found on the West Coast north of Port-aux-Basques.

b. *Gaylussacia dumosa*
Calopogon pulchellus
Habenaria blephariglottis

Four species with a much less oceanic distribution farther south have a very similar range in Newfoundland as the species of group Eb, viz. *Gaylussacia baccata, Carex folliculata, Habenaria orbiculata,* and *Dryopteris noveboracensis.*

Species which also have an oceanic distribution in America, *Lycopodium inundatum* and *Sphagnum pylaesii,* go much farther north along the Atlantic coast. The latter, especially, is often peculiarly abundant in bog pools on very cold peaks.

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[5]Until recently, *Sphagnum molle* was known from only two localities north of New Jersey, both on Newfoundland. Dr. W. S. G. Maass of the Atlantic Regional Laboratory, National Research Council, discovered the species on a number of localities in recent years, most of them on the Avalon and Burin Peninsulas.

F. RESTRICTED TO AVALON AND BURIN PENINSULAS.

Apparently an extreme form of group Eb.

Sphagnum macrophyllum[6]

This type of distribution is also found in many species which do not reach their northern limit in Newfoundland. Most conspicuous among them are some European species such as *Nardus stricta*, *Pedicularis sylvatica*, *Juncus bulbosus*, and *Sieglingia decumbens*. For some of them southeastern Newfoundland is their only foothold in North America.

G. SPECIES KNOWN FROM ONLY ONE OR TWO LOCALITIES.

Their occurrence is either due to accident or to historical factors. Obviously, they are not very well adapted to the climatic conditions and the competition relationships existing on the island.

Aster acuminatus	West Coast
Smilacina racemosa	
Mitchella repens	
Carex lacustris[7]	
Dryopteris marginalis[8]	
Scirpus maritimus	
Dennstaedtia punctilobula	
Myrica pensylvanica	South Coast
Oxalis montana	

PLANTS WITH ARCTIC OR SUB-ARCTIC AFFINITIES

The flora of Newfoundland contains a very considerable arctic element. Many of these species reach their southern limit at sea level in Newfoundland, and occur farther south

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[6]In 1962 Dr. W. S. G. Maass collected *Sphagnum macrophyllum*, thus far not known north of Nova Scotia, from five localities on the island, four of them on the Avalon Peninsula.

[7]Collected by Dr. R. Tuomikoski along the Harry's River in 1949.

[8]Occurs on a forested but unstable talus slope east of Barachois Pond. This station was discovered by the author in 1964.

only in alpine habitats, whereas others occur nowhere south of the island.

Their distribution in Newfoundland can largely be explained by a combination of climatic and edaphic factors, but lack of competition is an important factor for some species. In the following the factors thought to be controlling their distribution will be briefly discussed, followed by the description of a few typical distribution types.

CONTROLLING FACTORS

1. COMPETITION. It seems strange that more optimal physiological conditions, such as higher temperatures, should eliminate species in more southern latitudes. Therefore, the restriction of arctic species to northern latitudes is often believed to be a result of competition. The northern species, being species with a large temperature amplitude but unable to compete successfully with the more vigorous southern species, are expelled to areas with less severe competition.

2. HIGH SUMMER TEMPERATURES. Dahl (1951) lists a number of species which grow very poorly in botanical gardens at lower altitudes. He made the interesting observation that these species generally grow well in the autumn, and develop fine buds in spring. However, during the summer they become yellowish or brownish along the margins of the leaves, and after a few years they die. Dahl considers high summer temperatures detrimental to these species, and found a very good correlation between the isotherms of the annual maximum temperature and the southern limit of these species.

This intolerance for high temperatures also explains the occurrence of many arctic-alpine species in closed plant communities along the outer coast line far south of their inland range.

3. LIGHT REQUIREMENTS. Arctic species are plants of open, unforested areas, and usually they are species with high light requirements, unable to survive under shrub or forest canopy.

4. SOIL CONDITIONS. This affects the arctic element to the same extent as all other plant species. The distribution of serpentine and limestone has a very pronounced effect on the occurrence of a large group of species.

5. PHOTOPERIODISM. Little information is available on the effect of day length on the distribution of arctic species. However, its effect seems to be negligible with respect to our problem. This factor can at most prevent the occurrence of arctic species on Newfoundland, and it will certainly never cause the occurrence of an extremely long day plant at more southern latitudes.

6. ARIDITY OF CERTAIN COASTAL HABITATS. Fernald (1933, p. 123-7), commenting on the occurrence of the arctic element at sea level in northwestern Newfoundland, remarks that its presence is a result of the aridity and the calcareous nature of the soil rather than the coldness of the climate. The calcareous soils are undoubtedly an important factor governing the distribution of certain arctic plants, but it is hard to believe that the aridity of these sites is more important than the low summer temperatures. The coastal zone is remarkably cold, and the distribution of most species appears to be closely related to it. Those species whose restriction to the northwestern section of the Great Northern Peninsula does not appear to be controlled by low summer temperature only are also species of wet sites, such as *Carex microglochin, C. capitata, and C. chordorrhiza.*

7. CONTINENTALITY OF CLIMATE. The species mentioned above have a preference for continental climates. They may require low winter temperatures, or a rapid change from winter to summer. The warmer summers of continental climates can hardly play a role here. If this were the case, then these species would undoubtedly occur also at low elevations farther south along the west coast.

TYPES OF DISTRIBUTION

A. ON EXPOSED HEADLANDS ALONG THE COAST, EXPOSED PARTS OF THE BARRENS OF EASTERN NEWFOUNDLAND,

AND AT HIGH ELEVATIONS ELESWHERE, BECOMING PROGRESSIVELY MORE COMMON TOWARD THE NORTHERN PART OF THE LONG RANGE MOUNTAINS.

This type of distribution is shown by species which can find suitable soil conditions in any part of the province, i.e., they are species of acidic soils and those indifferent in this respect. They seem to be limited chiefly by high summer temperatures, but thrive well in both oceanic and more continental parts of the island.

Loiseleuria procumbens
Empetrum eamesii
Lycopodium selago
Carex bigelovii
Juncus trifidus
Arctostaphylos alpina
Sphagnum lindbergii
Cetraria cucullata
Alectoria ochroleuca
Diapensia lapponica
Silene acaulis[9]
Lycodium annotinum var. *pungens*
Betula borealis
Vaccinium uliginosum
Cetraria nivalis
Alectoria nigricans
Alectoria nitidula
Lobaria scrobiculata (as a ground inhabiting species)

B. RESTRICTED TO THE HIGHLANDS OF ST. JOHN, AND SOMETIMES A FEW OTHER HIGH AREAS IN THE WESTERN PART OF THE ISLAND.

This group consists of species of acid soils. Their occurrence is also chiefly controlled by summer temperatures, they require definitely lower temperatures than the species of Group A.

Salix herbacea
Sibbaldia procumbens
Deschampsia atropurpurea
Cassiope hypnoides
Phyllodoce caerulea
Hierochloe alpina

C. ALONG THE WEST COAST FROM ST. GEORGE'S BAY TO THE NORTHERNMOST TIP OF THE GREAT NORTHERN PENINSULA.

These species occur at higher elevations in the south but they come down to sea level in the northern areas. They are all basiphilic species, and their distribution is deter-

[9]Distinctly more common in limestone and serpentine areas.

mined by the occurrence of limestone or serpentine. Some are restricted to calcareous habitats (Ca), others occur on both serpentine and calcareous soils (Ca + Mg).

Oxytropis foliolosa (Ca)
Dryas integrifolia (Ca)
Carex terrae-novae (Ca)
Salix vestita (Ca)
Saxifraga aizoon (Ca)
Arenaria humifusa (Ca + Mg)
Potentilla nivea (Ca)
Arenaria rubella (Ca + Mg)
Salix cordifolia (Ca + Mg)
Cetraria tilesii (Ca)
Rhododendron lapponicum (Ca + Mg)
Hedysarum alpinum (Ca)
Carex rupestris (Ca)
Saxifraga oppositifolia (Ca)
Cerastium beeringianum (Ca + Mg)
Arenaria dawsonensis (Ca)
Armeria labradorica (Ca + Mg)
Kobresia simpliciuscula (Ca)
Castilleja septentrionalis (Ca + Mg)
Polygonum viviparum (Ca)
Solidago multiradiata (Ca + Mg)

D. RESTRICTED TO THE NORTHERN PART OF THE GREAT NORTHERN PENINSULA.

High summer temperatures appear to be the main factor limiting these species to this part of the island. Another factor, here vaguely described as continentality, is also important, at least for the first two species.

Carex chordorrhiza
Carex capitata
Salix reticulata (Ca)
Bartsia alpina (Ca)
Carex microglochin (Ca)
Pyrola grandiflora (Ca)
Primula egaliksensis (Ca)
Habenaria straminea (Ca)
Carex bicolor (Ca)
Saxifraga cespitosa (Ca)

E. RESTRICTED TO SERPENTINE AREAS.

The serpentine areas have a very sparse vegetation cover, and competition is of little importance on these sites. They are bleak, exposed habitats, locally with severe frost churning in fall and winter but the average summer temperatures

in the low lying areas (300-400ft.) are a few degrees higher than those prevailing in the coastal parts of southeastern Newfoundland. Evidently, these species do not require lower summer temperatures than the species of group A. They occur on these sites because of the lack of competition, the basic soils, and their ability to tolerate frost churning.

Lychnis alpina
Adiantum pedatum var. *aleuticum*

A large number of basiphilic species occur both on the serpentine and limestone soils (see under C). It should be realized that there are several other species limited to the serpentine soils which do not belong to the floral elements discussed in this paper.

F. SUB-ARCTIC HABITATS, BUT ALSO ON UNSTABLE SOILS, CLIFFS, AND RIVER BEDS AT LOWER ELEVATIONS.

Competition appears to be the main factor controlling the distribution of these species, although some of them require basic soils.

Trisetum spicatum	*Carex atrofusca*
Saxifraga aizoides	*Anemone parviflora*
Luzula spicata	*Carex scirpoidea*

Epilobium latifolium (known only from river gravels in Newfoundland.)

G. RATHER FREQUENT THROUGHOUT, ALTHOUGH DISTINCTLY MORE COMMON AT HIGHER ELEVATIONS.

A very large number of species belongs to this category. The following are a few examples.

Thalictrum alpinum	*Scirpus hudsonianus*
Rubus chamaemorus	*Carex capillaris*
Selaginella selaginoides	*Rubus arcticus*
Rubus acaulis	*Tofieldia pusilla*

A number of species show distribution patterns intermediate between the groups discussed above. Intermediate ranges between groups A and B are most common; to this category belong: *Betula minor*, *Betula glandulosa*, *Salix uva-ursi*, and *Carex rariflora*. All of them show a very marked

increase in abundance to the north, and they are rare or absent east of the Long Range Mountains.

Glacial and Post-glacial History as a factor in Explaining The Distribution Patterns

Most of the distribution patterns of northern and southern elements on the Island of Newfoundland can be explained adequately by the existing climatic and edaphic conditions. The ecological factors controlling this species distribution were analyzed in the previous section; in the following, the role of the historical factor will be discussed in more detail.

The importance of historical factors is often overemphasized in explaining the distribution of species (Böcher, 1943, 1951). Undoubtedly, the Wisconsin glaciation and the post-glacial climatic changes have had a pronounced influence on the composition of the present flora of Newfoundland, as they have had on the floras of all glaciated regions. There are probably a few species on the island today whose presence is the result of the post-glacial climatic optimum; there are others which may have taken advantage of the low sea level during late glacial times, and there are certainly many species which are absent due to the glacial epoch. However, it is well to remember that there is a large speculative element in all theories based on history. Often these theories are very attractive, but equally often it is not necessary to resort to far-fetched hypotheses to explain the present distribution of species, provided one pays proper attention to their ecology.

It is almost impossible to write about the origin of the Newfoundland flora, without mentioning the admirable pioneer work of Fernald. An extensive literature has built itself around his controversial theories, and the last word has certainly not been said about it. I will restrict myself to a very brief description of Fernald's ideas as far as they concern the subject of the paper, followed by my own views. A detailed discussion of this subject can be found in Marie-Victorin (1938), Raup (1941), Deevey (1949), Dahl

(1946), Dansereau (1950), Wynne-Edwards (1937-1939), Rousseau (1949). A discussion on the distribution and the origin of the so-called "Cordilleran" element in the flora of Newfoundland has been omitted here on purpose since the problem is of an entirely different nature.

A point of interest in Fernald's theories on the origin of the Newfoundland flora (1911, 1918a, 1918b, 1925, 1926, 1933) is his explanation of the presence of the Coastal Plain element. In his early writings, Fernald (1918) believed that the Coastal Plain element had migrated northward toward the end of the glacial period over a land bridge, approximately following the continental shelf. This land bridge was very sandy, and only species with low nutrient requirements could use it. Thus it was well suited for the species of acid soils which make up the Coastal Plain element but not for other southern species.

Later Fernald (1933, p. 95-107) revised this theory, mainly since his nunatak theory (Fernald, 1925), as an explanation of the occurrence of the Cordilleran element in eastern Canada, had received so much approval of both geologists and botanists, whereas his post-glacial land bridge theory had few supporters. He postulated that the Coastal Plain species had reached Newfoundland during the Tertiary period over the then emerged continental shelf. Subsequently, they survived the glacial period on nunataks, unglaciated refugia occurring as islands in the continental ice sheet.

At present it is obvious that all of Newfoundland, including its highest peaks, has been covered with ice at some time or another during the glacial epoch (MacClintock and Twenhofel, 1940). The other nunatak areas in northeastern North America are equally unjustified (Flint et al., 1942; Odell, 1938; Abbe, 1936; Deevey, 1949). In addition to this, many so-called nunatak indicators have been found in the "gap" of the Canadian Shield during recent years (Rousseau, 1948, 1949; Scoggan, 1950; Raymond, 1950). Although the existence of genuine nunataks on Newfoundland is extremely unlikely, it is quite well possible that certain

floral elements survived the glaciation in coastal habitats, especially along the Atlantic shore.

However, it is not necessary to resort to such speculations to explain the distribution of these species. The Coastal Plain element does not appear to be a relic flora, which is restricted to the bleak eastern and southern parts of the island owing to the occurrence of acidic soils (Fernald, 1911, 1918). In my opinion, it occurs on Newfoundland because it is made up of oceanic and sub-oceanic species which are unable to tolerate the severe winters of most of the adjacent continent. Severe snow drifting in the barren areas may even permit these species to occur farther inland than would be otherwise possible. A few species with an unusual gap in their distribution, e.g. *Sphagnum molle* and *S. macrophyllum*, could well have covered more of the island during the post-glacial climatic optimum.

A second point of interest in Fernald's theories is his explanation of the absence of many species of nutrient-rich soils occurring commonly on the adjacent Canadian mainland. He attributed their absence to the inability of these species to cross the Cabot Strait between Cape Breton Island and Newfoundland. He reasoned further, that owing to their higher demands on soil fertility these species could not make use of the land bridge as the Coastal Plain species did. "Thus", he states, "typical Canadian plants, unless their range extends to the north side of the Strait of Belle Isle[10], are absent from the island" (Fernald, 1911).

Clearly this point of view cannot be defended any longer. A large group of species, notably those with high nutrient requirement in groups A, B, C, and D do not occur on the Northern Peninsula and consequently they must have reached Newfoundland from the south (see also p. 32). Thus the Cabot Strait cannot be considered a very effective barrier.

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[10]This Strait separates Newfoundland from southern Labrador; it is only eleven miles at its narrowest point and thus it can be much easier bridged by diaspores than the seventy mile wide Cabot Strait.

Those species present on the adjacent mainland (Roland, 1942; Dore and Roland, 1941) but absent on the Island of Newfoundland are all species of tolerant hardwood forests, e.g., *Acer saccharum*, *Fagus grandifolia*, *Epifagus virginiana*, *Quercus borealis*, *Ulmus americana* and *Sanguinaria canadensis*.

Even in the climatically favorable southwestern part of Newfoundland the vegetative season starts almost two weeks later than in Cape Breton Island. Therefore, it seems more reasonable to attribute the absence of these species to the shortness of the vegetative season rather than to their inability to cross the Cabot Strait.

On Newfoundland the drier alder thickets are the habitats most closely resembling the tolerant hardwood forests. It is interesting to note that the few tolerant hardwood species which do reach Newfoundland all occur in alder thickets, e.g., *Claytonia caroliniana* and *Smilacina racemosa*.

There is one group of species with southern affinities whose distribution is rather enigmatic. It includes species as *Pinus resinosa*, *Carex houghtonii* and *Gaultheria procumbens* (Group Cb) but also *Chimaphila umbellata*[11]. All of them occur on a number of widely separated or isolated stations where they can be very common. It is difficult to understand the present distribution of these species without assuming that they once covered a larger part of the island. This could have been the case during a warm post-glacial period. Evidence for such a climatic optimum has been collected for other parts of northeastern America (Deevey, 1949). Livingstone and Livingstone (1958) and Schofield (1960) have shown that a distinctly warmer period has occurred on Cape Breton Island. During this period. *Quercus* and several other hardwoods were much more common than today, and even *Carya* pollen has been found in these

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[11]Recent addition to the flora of Newfoundland. Collected by R. S. van Nostrand at New Bay Lake (central Newfoundland), and by the author near Flat Bay Brook (West Coast), both in 1958. There is an unverified record of its occurrence near Hall's Bay.

deposits. This period was followed by a slightly cooler and more humid period in which *Tsuga* was a prominent component of the forest, and from then on the climate gradually deteriorated.

Although no evidence for a climatic optimum is available for Newfoundland, it seems reasonable to assume that this warmer climate also affected the island, thus creating conditions for a more widespread occurrence of species such as *Pinus resinosa*. In the absence of pollen analytical studies or fossil records from Newfoundland we can only speculate on this subject. It can only be said with confidence that the present climatic conditions are unfavorable for these species for otherwise they would have spread from their present locations. The latter applies also to the southern species which are known from a single locality only (Group G.) *Oxalis montana*, a species restricted to LaPoile Bay, an isolated bay on the south coast may be an exception in this respect. It has to cross a large area of bleak barren land to reach the forests of the west coast, and it is conceivable, though unlikely, that this is the reason for its absence from the rest of the island.

The occurrence of a post-glacial climatic optimum on Newfoundland may throw some doubt on the previous statement that some of southern species in groups A, B, C, and D must have reached the island across the Cabot Strait. Could not their northern limit have occurred in Labrador during this warm period, so that they could have crossed the Strait of Belle Isle and spread into Newfoundland from the north? Wenner's (1947) pollen analytical studies in Labrador and northern-most Newfoundland seem to indicate that this is very unlikely. He found no evidence of important climatic changes after the area became covered with a forest vegetation. Presumably, the hypsothermal period occurred before the climate in southern Labrador had ameliorated sufficiently to permit the growth of a forest vegetation.

The widespread occurrence of a great number of arctic and sub-arctic species occurring on the island can be satisfactorily explained by the climatic conditions, as has been

done in the description of the distribution types. Their common occurrence at sea level in coastal areas is due to the very low summer temperatures prevailing in these regions. Temperature measurements with sucrose ampoules (Pallmann *et al*, 1940) carried out by the author in 1961, have shown that the average temperatures during the vegetative season in coastal barrens are equal to those on the highest peaks of the Table Mountain at Bonne Bay, the Lewis Hills and the Gaff Topsails.

A peculiar mingling of arctic and southern species can be seen in the coastal habitats, as already remarked by Fernald (1911). However, in the author's opinion this is a result of the present day climatic conditions rather than the presence of a relic Coastal Plain element in an essentially northern vegetation. The arctic species occur there because of the low summer temperatures, whereas the Coastal Plain species are present because of the oceanic climate, and in spite of the low summer temperatures to which they are adapted.

Summary

The flora of Newfoundland contains many species with northern and southern affinities. The ecological factors controlling the distribution of these floral elements are discussed in some detail followed by a description of the distribution patterns within Newfoundland.

Most of the species distributions can be satisfactorily explained by the present climatic and edaphic conditions. The Coastal Plain element, should not be considered as a relic flora restricted to southern Newfoundland because of soil conditions but rather as a flora consisting of oceanic species unable to tolerate extreme winter temperatures.

The absence of some southern species, notably those of northern hardwood forests should be attributed to unfavorable climatic conditions and the absence of the hardwood forest floor habitat rather than to isolation. The number of species which did reach Newfoundland across the Cabot

Strait is so great that it can hardly be considered an effective barrier for most species.

The peculiar distribution of *Pinus resinosa, Chimaphila umbellata, Gaultheria procumbens* and *Carex houghtonii* can only be explained by assuming that these species were widespread during the post-glacial climatic optimum. The subsequent deterioration in climate restricted these species to a few isolated areas with relatively warm soils.

SOMMAIRE

La flore de Terre-Neuve comprend un grand nombre de plantes du sud et de plantes arctiques et arctiques-alpines. Les facteurs écologiques que régissent la répartition des éléments de la flore de l'île font l'objet d'une étude détaillée que l'auteur fait suivre d'une description du mode naturel de répartition des diverses plantes dans l'île de Terre-Neuve.

Pour la plupart des plantes, la répartition des espèces peut être attribuée ans crainte d'erreur aux conditions locales actuelles du climate et du sol. La flore de la plaine côtiére ne doit pas être regardée comme une flore reliquale restreinte au sud-est de Terre-Neuve par suite des conditions particulières du sol, mais plutôt comme une flore composée d'espèces océaniques qui ne peuvent pas survivre aux températures hivernales extrêmes.

L'absence de certaines espèces du sud, l'absence notamment de certaines espèces des forêts de feuillus du nord, est attribuable aux conditions climatiques défavorables et à l'absence du milieu caractéristique des forêts de feuillus, plutôt qu'a l'isolement. Le nombre d'espèces qui se sont établies dans l'île de Terre-Neuve après avoir traversé le détroit de Cabot est tellement éléve que l'on croit difficilement que le détroit puisse constituer un sérieux obstacle à la propagation de la plupart des espèces.

La répartition bizarre des espèces *Pinus resinosa, Chimaphila umbellata, Gaultheria procumbens et Carex houghtonii* ne peut être attribuée que à la répartition de ces espèces dans toute l'île durant une période post-glaciaire, alors que

les conditions climatiques étaient les plus favorables à leur reproduction. Le climat beaucoup plus rude qui a suivi cette période a confiné la survivance de ces espèces dans quelques poches isolées où le sol est rélativement moins froid.

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LITERATURE CITED

ABBE, E. C. 1936. Botanical results of the Grenfell-Forbes Northern Labrador Expedition, 1931. Rhodora **38:** 102-164.

AHTI, T. 1959. Studies on caribou lichen stands of Newfoundland. Ann. Botan. Soc. Zoo. Botan. Fennicae "Vanamo" **30:** (4) : 1-44

ARSÉNE, L. 1927. Contribution to the flora of the islands of St. Pierre et Miquelon. Rhodora **29:** 117-133, 144-158, 173-191, 204-220.

BOCHER, T. W. 1943. Nordische Verbreitungstypen. Svensk Bot. Tidskr. **37:** (4) : 352-370.

———. 1951. Distributions of plants in the circum-polar area in relation to ecological and historical factors. J. Ecology **39:** (2) : 376-395.

DAHL, E. 1946. On different types of unglaciated areas during the ice ages. New Phytologist **45:** 225-242.

———. 1951. On the relations between summer temperature and the distribution of alpine vascular plants in the lowlands of Fennoscandia. Oikos **3:** (1) : 22-52.

DANSEREAU, P. 1950. Flora and vegetation on the Gaspé Peninsula. Wild Flower, April **1950:** 26-39.

DEEVEY, E. S. 1949. Biogeography of the Pleistocene. Bull. Geol. Soc. Am. **60:** 1315-1416.

DORE, W. G. and A. E. ROLAND. 1941. The grasses of Nova Scotia. Nova Scotian Inst. Sci. Proc. **20:** 177-288.

FERNALD, M. L. 1911. A botantical expedition to Newfoundland and Southern Labrador. Rhodora **13:** 109-162.

———. 1918a. The geographic affinities of the vascular floras of New England, the Maritime Provinces and Newfoundland. Am. J. Botany **5:** 219-236.

———. 1918b. The contrast in the floras of Eastern and Western Newfoundland. Am. J. Botany **5:** 237-247.

———. 1924. Isolation and endemism in Northeastern America and their relation to the age and area hypothesis. Am. J. Botany **11:** 558-572.

_____. 1925. Persistence of plants in unglaciated regions of boreal America. Mem. Amer. Acad. Sci. N. S. **15:** 237-342.

_____. 1926. Two summers of botanizing in Newfoundland. Rhodora **28:** 49-63, 74-87, 89-111, 115-129, 145-155, 161-178, 181-204, 210-225, 234-241.

_____. 1933. Recent discoveries in the Newfoundland flora. Rhodora **35:** 1-16, 47-63, 80-107, 120-140, 161-185, 203-223, 231-247, 265-283, 298-315, 327-346, 364-384, 395-403.

FLINT, R. F., M. DEMOREST, and A. L. WASHBURN. 1942. Glaciation of Shickshock Mountains, Gaspé Peninsula. Bull. Geol. Soc. Am. **53:** 1211-1230.

HARE, F. K. 1952. The climate of the Island of Newfoundland. Can. Dep. Mines Tech. Surv., Geogr. Bull. **2:** 36-88.

LIVINGSTONE, D. A. and B. G. R. LIVINGSTONE. 1958. Late glacial and post-glacial vegetation from Gillis Lake in Richmond County, Cape Breton Island, Nova Scotia. Am. J. Sci. **256:** 341-359.

MACCLINTOCK, P. and W. H. TWENHOFEL. 1940. Wisconsin glaciation in Newfoundland. Bull. Geol. Soc. Am. **51:** 1729-1756.

MARIE-VICTORIN, FRÈRE. 1938. Phytogeographical problems of Eastern Canada. Am. Midland Naturalist **19:** (3): 489-558.

ODELL, N. E. 1938. The great ice age and its effects. *In* Forbes, A. Northernmost Labrador mapped from the air. Am. Geol. Soc. Spec. Publ. **22:** 204-215.

PALLMAN, H., E. EICHENBERGER, und A. HASLER. 1940. Eine neue Methode der Temperaturmessung bei ökologischen und bodenkundlichen Untersuchungen. Ber. Schweiz. Botan. Ges. **50:** 337-362.

RAUP, H. M. 1941. Botanical problems of Boreal America. Botan. Rev. **7:** 147-248.

RAYMOND, M. 1950. Esquisse phytogeographique du Québec. Mem. Jard. Bot. Montreal **5:** 1-147.

ROLAND, A. E. 1942. The flora of Nova Scotia. Nova Scotian Inst. Sci. Proc. **21:** 95-642.

ROULEAU, E. 1956. A check-list of the vascular plants of the Province of Newfoundland. Contr. Inst. Bot. Univ. Montreal **69:** 41-106.

ROUSSEAU, J. 1948. The vegetation and life zones of George River, Eastern Ungava, and the welfare of the natives. Arctic **1:** (2): 93-106.

_____. 1949. The value of botany as indicator of unglaciated areas. Pacific Science Congr. New Zealand. Feb. 1949.

ROWE, J. S. 1959. Forest regions of Canada. Can. Dep. Northern Affairs Nat. Resources, Forestry Branch Bull. **123:** 71 p.

SCHOFIELD, W. B. and H. ROBINSON. 1960. Late-glacial and post-glacial plant macrofossils from Gillis Lake, Richmond County, Nova Scotia, Canada. Am. J. Sci. **258:** 518-522.

SCOGGAN, H. J. 1950. The flora of Bic and the Gaspé Peninsula, Québec. Nat. Museum Canada, Bull. **115:** 399 p.

WENNER, CARL-GOSTA. 1947. Pollen diagrams from Labrador. Geografiska Annaler **29:** (3-4): 137-373.

WYNNE-EDWARDS, V. C. 1937. Isolated arctic-alpine floras in eastern North America. Roy. Soc. Can. Trans. 31, Sec. V, ser. **3:** 1-26.

_____. 1939. Some factors in the isolation of rare alpine plants. Roy. Soc. Can. Trans. 33, Sec. V, ser. **3:** 35-42.

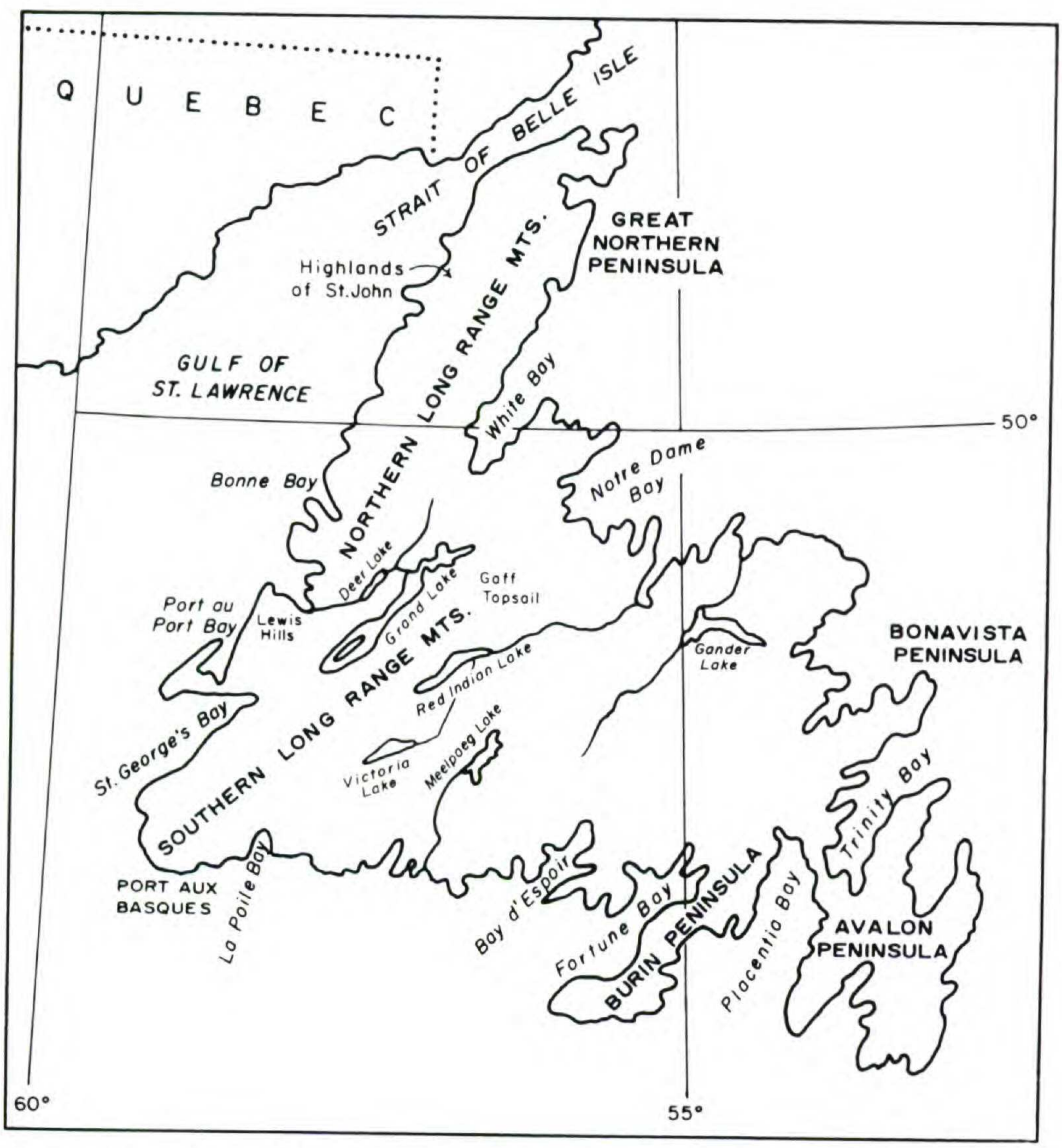

Figure 6. Map of Newfoundland showing geographical features mentioned in text.